

The Systematics of the Genus *Dira* Huebner (Lepidoptera: Satyrinae), with a Description of a New Subspecies of *D. clytus* (Linnaeus)

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No. 3

Evolution and distribution

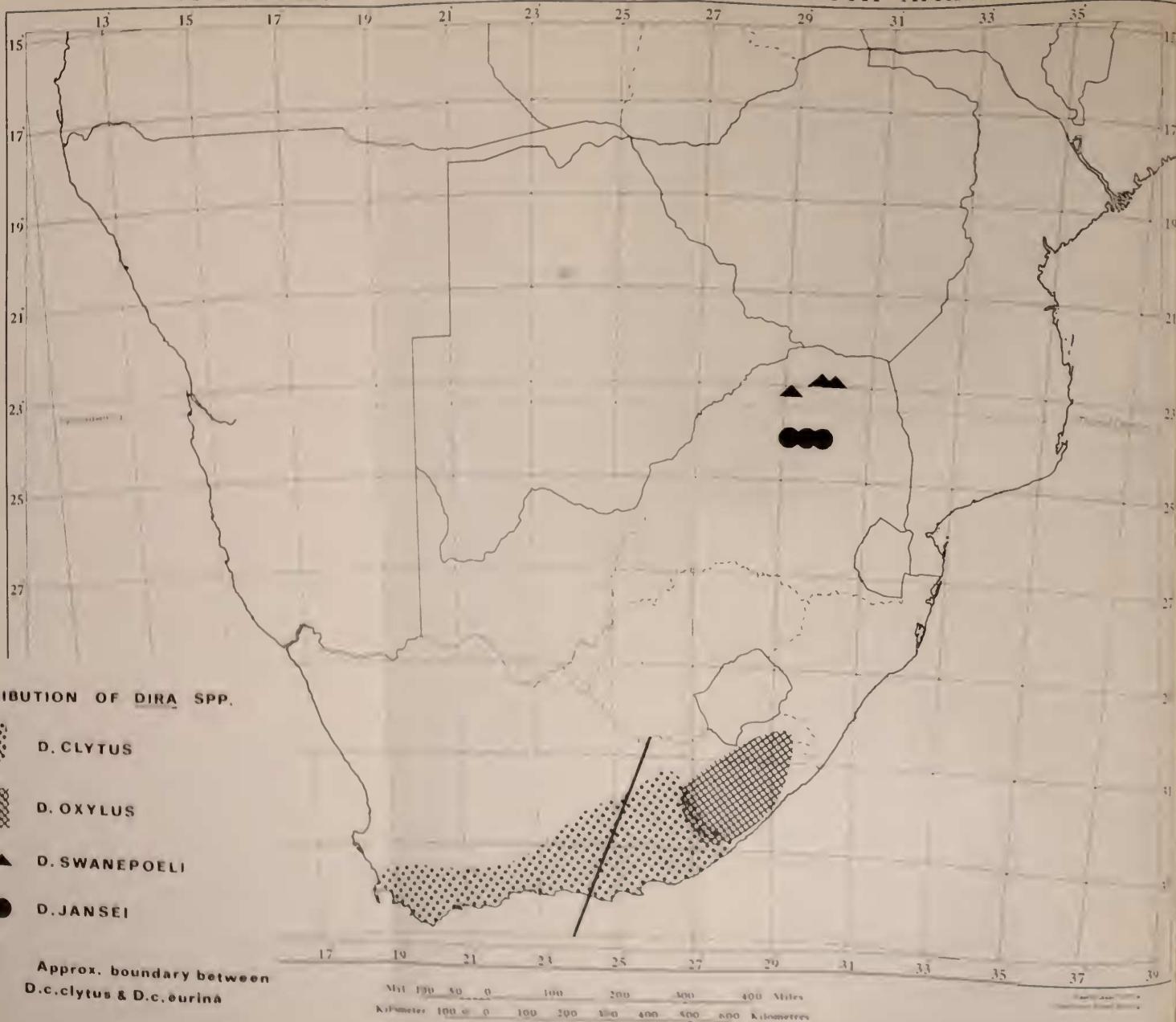
This interesting endemic South African genus comprises four, allopatric, species ranging eastwards in an arc from the western Cape Province to the Transkei, then northwards to the Transvaal. Due to the general inordinate abundance of individuals of the species and that their foodplants are grass *spp.*, a widespread distribution potential exists. This is fully realised only in the species *D. clytus* as it ranges almost continuously along a wide coastal strip from the extreme western Cape Province to the mid-eastern Cape. At this point the distribution of *clytus* is abruptly terminated where it makes contact with the next species *D. oxylus* (Trimen) which continues eastwards occupying the greater part of the Transkei.

Much more restricted in range than *clytus*, *oxylus* extends up to, but inexplicably, does not penetrate Natal. The distribution of the third species, *D. swanepoeli* (van Son), poses even greater vexing questions of evolutionary history in that despite bearing a remarkably close resemblance to both *clytus* and *oxylus* it is separated from these two species by a distance of some 825 km. Even more restricted in range than *oxylus*, *swanepoeli* occurs only in a few limited localities on the Zoutpansberg mountains, north of Louis Trichardt in the northern Transvaal. The fourth and last species, *D. jansei* (Swierstra), is placed *c.* 150 km. south of *swanepoeli* and occurs very locally over mountains from Potgietersrust eastwards to the western slopes of the Wolkberg. It is more sharply differentiated in facies from any of the other species than they are from each other.

The entire distributional pattern is thus one of a vast population continuum in the Cape Province formed by *clytus* and *oxylus*. This is followed by a huge gap from *c.* latitudes 30° to 25° S., whereupon widely scattered relicts of the genus re-appear on the mountains of the Transvaal in the form of *swanepoeli* and *jansei*.

Except perhaps for *clytus*, the *Dira* spp. could be a declining group, with possible extinction threatening at least the two Transvaal isolates. The species-group doubtless enjoyed a more continuous and wider distribution in the fairly recent past as evidenced by the close resemblance between *clytus*, *oxylus* and *swanepoeli*. The diminution and fragmentation of populations we see today was doubtless effected by past changes in topography and consequently habitat. Suitable ecological conditions persisting on certain isolated mountain ranges could account for the survival of some population remnants in the form of the montane species *swanepoeli*,

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oxylus and *jansei*. Sufficiently prolonged isolation allowed the various species to evolve and in time the distributional hiatus between *clytus* and *oxylus* was closed. As will be seen, reproductive isolation between these two species is still in the process of consolidation, as hybridisation sporadically occurs.

Ecology

Dira species are apparently stimulated to emerge by the first major drop in temperature heralding the approach of winter. This would explain why in the eastern Cape at Stutterheim, *clytus* emerges at c. 900 m. altitude a month and a half earlier than at sea level only 80 km. away, where it remains warmer at the approach of winter. Although at high altitudes *oxylus* may emerge early in January, the majority of populations of the various species are only on the wing from about February to March/April, continuing even into May in the case of *clytus* in the Cape Peninsula.

Generally extremely common and widespread during their autumn flight period, *clytus* and *oxylus* tend to aggregate into colonies from which some individuals occasionally stray. The dense mass of males within a colony fly about just above grass level in a lazy buoyant manner, evidently intent on locating females which spend much time either resting or else scattering their eggs about, among the grass stalks. This manner of oviposition is possibly unique in *Dira* and *Dingana* van Son species.

The beginning and end of this flight period is comparatively abrupt and the nine-month interval before the next emergence is characterised by a complete absence of the adult insect. Interestingly, it happens on rare occasions that this natural regulation in its life-cycle breaks down causing individuals to hatch out of season. This was encountered only at Knysna where during late December two examples of *clytus* were seen flying about on two separate occasions.

The daily flight period begins early, from about 8 a.m., and as it becomes warmer towards midday there is a decline in activity. This avoidance of excessive sunlight is reflected in the choice of habitat, situated typically about open scattered trees.

The ecology of *Dira swanepoeli* and *jansei* corresponds basically to *clytus* and *oxylus*, but according to D. Whiteley of Durban, *swanepoeli* is not so partial to the shade of trees and also has a rather faster more purposeful flight, settling more often, usually among grass and rocks. *D. jansei*, although partial to shade, apparently has a different flight pattern, more reminiscent of a species of *Coenyra* Hewitson than a *Dira*.

Taxonomy

Abbreviations used to refer to wing surfaces in descriptions are: *Fw.* & *Hw.*: fore- and hind-wings. *Up.* & *Un.*: Upperside and underside. *UpFw.* & *UpHw.*: Upperside of fore- and hind-wings. *UnFw.* & *UnHw.*: Underside of fore- and hind-wings.

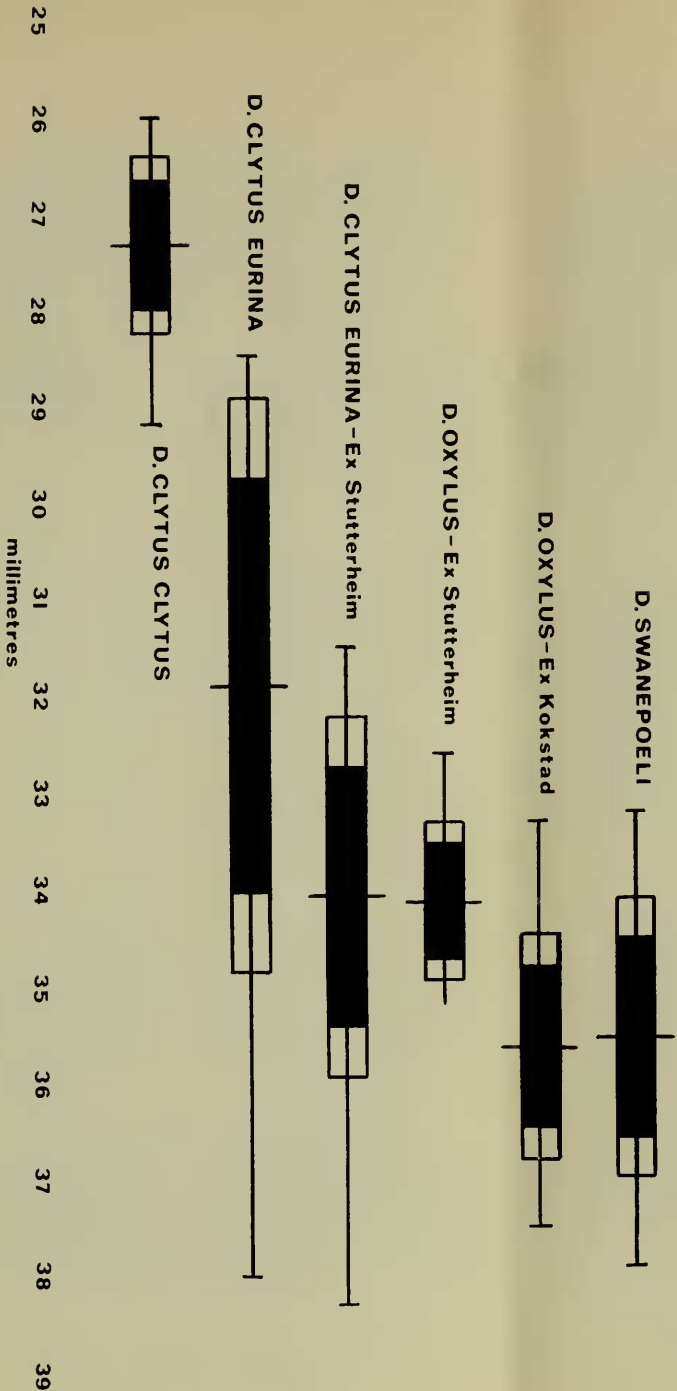


Fig. 1. Population samples (each consisting of 10 specimens) of three *Dirca* species, illustrating an eastward (but not northward) size increase in successive populations. Size estimate was gauged from length of right forewing (base to apex). Median vertical lines indicate the mean, horizontal lines the sample range, open rectangles the standard deviation, solid black rectangles 95% confidence intervals for the mean.

PLATE II

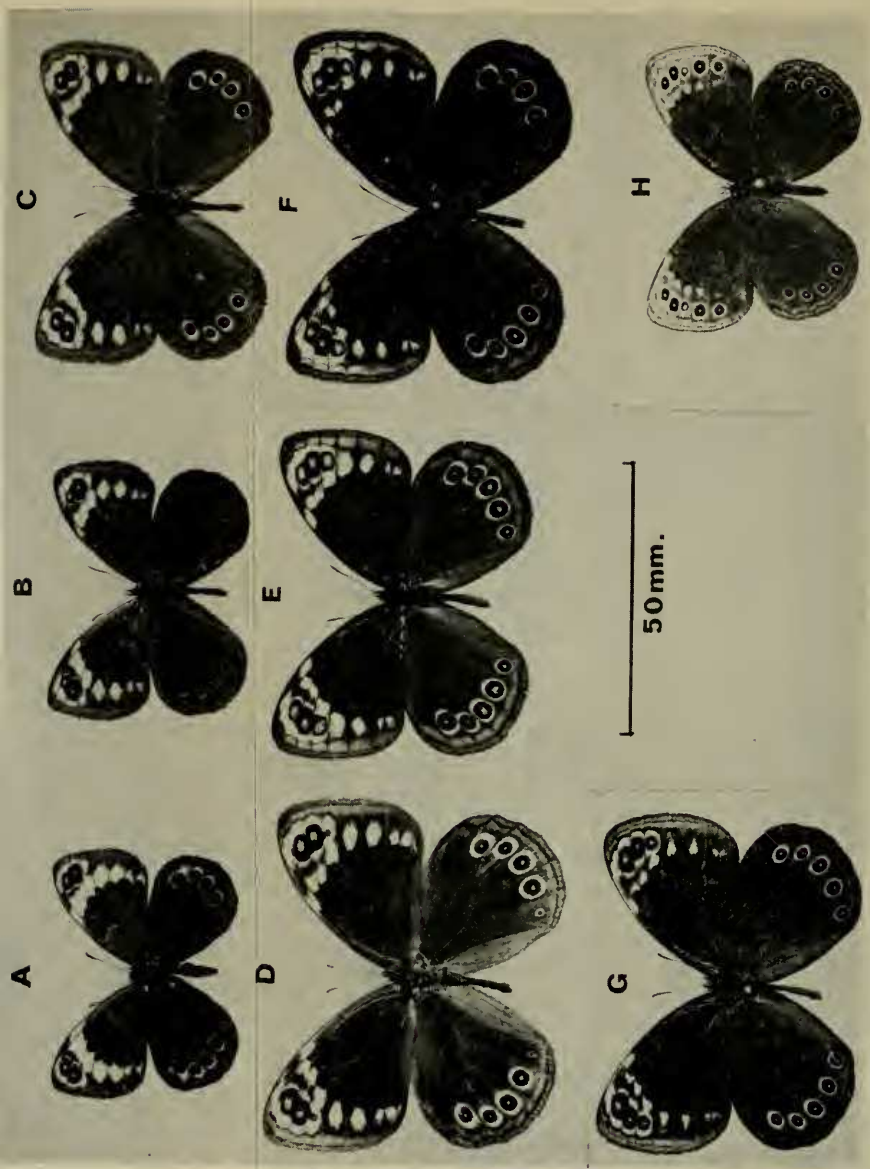


Fig. IV. Uppersides of male *Dira* species.

(A) *D. clytus*: Cape Town. (B) *D.c. clytus*: Plettenberg Bay. (C) *D.c. eurina*: Holotype, Grahamstown. (D) *D.c. eurina*: Stutterheim. (E) *D. oxylus*: Stutterheim. (F) *D. oxylus*: Kokstad. (G) *D. swanepoeli*: Louis Trichardt. (H) *D. iansea*: Chintsaenenort.

It has long been known that the *D. clytus* populations of the eastern Cape are quite different from the smaller darker counterparts occupying the more western parts of the range. Trimen (*South African Butterflies*, Vol. 1, 1887, p. 93), first drew attention to this, referring to the eastern form merely as "Var. A" (Grahamstown, Cape Colony). In his second volume of the series *The Butterflies of Southern Africa*, pp. 58-59 (Transvaal Museum, 1955), G. van Son accorded no nomenclatural recognition to Trimen's "Var. A", except to mention that eastern populations differed in a few minor characters. In order to resolve the matter fully, some 250 specimens of *D. clytus* have, over the years, been specially collected from as many points within its range as possible.

It was at once evident that the extreme western and eastern forms are indeed very dissimilar in facies. The intervening populations occurring from about Mossel Bay to the Tsitsikama forests in the southern Cape exhibit rather irregular clinal transition, resulting in some more easterly-situated populations showing greater affinity to extreme western Cape material than those inhabiting areas in between. Despite this profuse, rather discordant variation, these southern Cape populations may clearly be grouped with western Cape material which typically have a broad band of cream spots running in an arc from the *UpFw.* costa to the inner margin. In more than 75% of cases these spots are either broadly confluent or nearly so, seldom completely separate as in eastern Cape specimens. In specimens from the Peninsula the spots form a particularly broad band giving this form a distinctive appearance (see Plate II, fig. IV). The spots of this band become smaller and more widely separated in examples from about the Gouritz River (near Mossel Bay) eastwards. However, in most cases they are either still just in contact with each other or nearly so. Populations of *clytus* continue to be essentially similar right up to at least the Storms River in the Humansdorp district, i.e. with the individuals being small and dark, and with the rings surrounding the *UpHw.* ocelli narrow and rust-tinged, usually ill-defined in a photograph (see Plate II, fig. IV). The length of the *Fw.* in all these western and southern cape populations does not appear to exceed 30 mm. From about Humansdorp, the Gamtoos River and especially from Uitenhage and eastwards, specimens show the typical characteristics of the eastern race, in which the spots of the cream band become well separated. The rings bounding the outer edges of the ocelli of the *UpHw.* become lighter, i.e. cream in colour, and also often wider so that they are easily seen in a photograph (see Plate II, fig IV). Progressive size increase eastwards results in few eastern Cape specimens measuring less than 30 mm. in the *Fw.*, while some of the largest from Stutterheim at the extreme end of their distribution even exceed 38 mm., a size not attained by any known individuals of the other *Dira* species.

It is evident that the entire eastward inclined character shift affecting *clytus* is of a nature that effects a link-up with *oxylus*. Thus many of the characters distinguishing eastern forms of *clytus* are shared by adjacent populations of *oxylus* so that the two species here bear a close resemblance to one another, so much so that at first I considered the two forms to be conspecific. Every criterion that has ever been used to separate *oxylus* from *clytus* breaks down in particular specimens from these contiguous populations and the only character that has been found in all cases to be reliable in separating the two is a minor feature of the male genitalia, viz the juxta (see Plate III, fig. II).

However, it was decided to regard the two forms as separate species for the following reasons:

(a) Both in habitat and in times of emergence *oxylus* and *clytus* show unique characteristics. At Stutterheim *oxylus* hatches at a particular spot promptly at the end of January, whereas in a colony of *clytus* not more than two km. away emergence is remarkably regulated to within a few days either way of the 18th February, by which time *oxylus* is already dwindling in numbers.

(b) Populations of both species in these areas of overlap aggregate into separate colonies, with no apparent mixing. *D. oxylus* colonies tend to be situated on grassy mountain slopes, whereas those of *clytus* centre more on flatter, low-lying ground, and generally in association with trees, often those of a plantation.

(c) It is obvious that in adjacent populations of *clytus* and *oxylus* a fair amount of hybridization does take place (see Plate IV, fig. III). However, judging by the fact that in the vast majority of cases it is possible by using external characters to differentiate between specimens of each species from all parts of their ranges, it is also obvious that these hybrids are being selected against by various factors such as the above-mentioned behavioural incompatibility.

Ecological discontinuities no doubt also play a part in suppressing allopatric hybridization in this zone of contact between *clytus* and *oxylus*. Thus *clytus* appears to favour the sweeter grasses while *oxylus* appears to follow the distribution of the sourveld. The boundaries separating these grass types coincide with the zone of contact between *clytus* and *oxylus* from Queenstown down through Stutterheim.

Genetic incompatibility possibly plays a minor role in preventing appreciable introgression between *clytus* and *oxylus*. Support for this view is provided by the lack of constant character differences between the two taxa, except in a very minor feature of the male genitalia, and that clinal patterns are the same for both species. Everything considered, the *clytus/oxylus* zone of contact is a narrow one, and even though secondary contact between the two was established before full reproductive isolation was attained, they have diverged sufficiently for each to maintain themselves as separate species over virtually their entire range.